Plant Physiol. (1971) 48, 631–636

Immediate and Subsequent Growth Responses of Maize Leaves to Changes in Water Status[1]

Received for publication January 4, 1971

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ABSTRACT

Elongation of intact young leaves of maize was found to be dynamically dependent on soil water supply. With adequate water, elongation was remarkably constant but slowed when the water potential of the soil in pots dropped from −0.1 to −0.2 bar and stopped when it dropped to −2.5 bars. The corresponding range of leaf water potential was −2.8 to −7 bars. Elongation resumed in less than a few seconds after a mildly water-stressed plant was rewatered.

The effects on leaf elongation of step-wise changes in water potential of the root solution were determined. When the water potential of the root medium suddenly decreased below 0 bar, growth stopped initially and then resumed at a lower rate. When the water potential was suddenly increased back to 0 bar, growth accelerated transitorily to a high rate before slowing to the steady state rate. These results suggest an increase in cell extensibility during water stress.

Leaves stressed for 1 or more days attained after rewatering almost the length of the control leaves. Growth rate after rewatering did not exceed that of the control at the corresponding developmental stage except during the short transitory rapid phase lasting only a fraction of an hour.

As stress developed, growth stopped before carbon dioxide assimilation decreased noticeably. Upon the release of mild and short stress, the transitory rapid growth completely made up for the reduced elongation during stress, suggesting that metabolic processes for cell expansion might have proceeded unchecked during the stress period.

The sensitivity and rapidity of response to changes in water status all point to the direct role of water in growth; its uptake provides the physical force for cell enlargement.

Recent studies have reaffirmed the importance of turgor pressure and favorable water status in the growth of plant cells. With *Nitella* internodal cells, Green (10) elegantly demonstrated a close dependence of growth on turgor pressure. The direct monitoring of turgor pressure and the detailed recording of increase in cell size after step-wise changes in the solute potential of the external medium permitted the analysis of growth in terms of cell extensibility. With higher plants the direct measurement of turgor pressure is not yet possible. Boyer (4) was able to follow accurately the water potential (Ψ) of enclosed leaves during recovery from water deficiency and found that growth was intimately linked with leaf Ψ and with calculated turgor pressure. However, he had to estimate short term growth from the rate of water uptake by excised leaves and therefore was not able to delineate transitory changes in growth associated with rapid changes in plant water status. We (13) developed a method of measuring growth of intact leaves of monocotyledonous plants on a minute-by-minute basis and briefly reported that leaf growth resumed immediately when a mildly water-stressed plant was watered. A transitory phase of rapid growth was observed after watering.

This study was undertaken to quantify in some detail the growth responses of an intact higher plant to varying water supply with particular emphasis on the short term and dynamic aspects. These aspects were hitherto largely unexplored because suitable methods were lacking.

MATERIALS AND METHODS

Plant Material. Maize plants (*Zea mays* L., var. WF9 × M14, Crow's hybrid corn, Milford, Ill.) were grown in a growth chamber as before (13) with 15 hr of light (1100 ft-c, 30 C) and 9 hr of darkness (22 C). All measurements were made during the light period. When grown in soil, seedlings were thinned after emergence to four uniform plants per pot. Each pot (10 cm in diameter) contained 500 g of air-dried Columbia silt loam. The soil was irrigated when its Ψ dropped to about −0.3 bar, as estimated from the moisture desorption curve (unpublished data). For nutrient solution culture, seedlings were grown in aerated one-tenth strength Hoagland solution.

Measurement of Leaf Elongation and Water Potential. The method of measuring the elongation of an intact leaf with high resolution has been detailed (13). The base of the plant was anchored by the soil or by clamping the mesocotyl of plants growing in nutrient solution. The apex of the leaf was attached to the core of a LVDT[3] (1.3-cm stroke) so that, as the leaf elongated, a millivolt output, proportional to the displacement of the apex, was produced.

One difficulty encountered was the increasing tendency, with frequent or continuous use, of the core of the LVDT to stick to the transformer cylinder. Reducing the line voltage (to as low as 7 v) reduced sticking but did not eliminate it.

[1] This work was supported in part by Grant B-029-CAL from the Office of Water Resources Research, United States Department of Interior; by a grant from the Water Resources Center, University of California; and by National Science Foundation Grant GB 5658.

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[3] Abbreviation: LVDT: linear variable differential transformer.

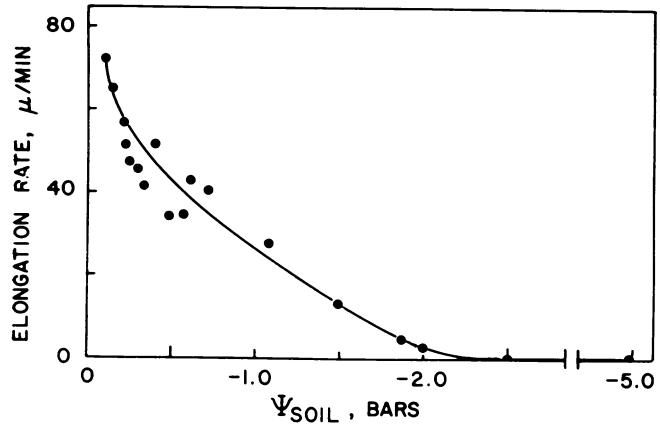

FIG. 1. Rate of leaf elongation as affected by soil Ψ. Points represent single measurements taken in the growth chamber on the youngest (third) leaf of 10-day-old plants. Relative humidities were 32 and 71%, respectively, for the light and dark periods. See text for other conditions. Some of the elongation rates are given again in relation to leaf Ψ in Figure 2.

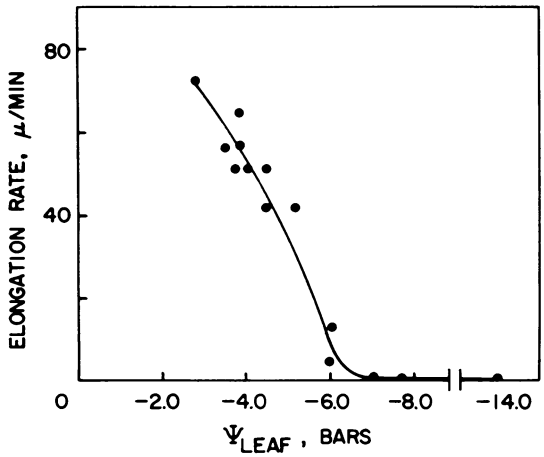

Fig. 2. Rate of leaf elongation in relation to leaf Ψ. Points are single measurements taken in the growth chamber. Elongation was of the youngest (third) leaf, whereas Ψ was of the second leaf of 10-day-old plants. In separate experiments, Ψ of the youngest leaf was found to be within 1.5 bars of the Ψ of the next older leaf at several stress levels.

Sensitivity had to be increased to compensate for the reduced input. A better solution, though still partial, was to have several LVDTs so that each was used alternately for a few days and rested for several weeks.

Leaf Ψ was determined by the Shardakov method (2). While the elongation of the youngest expanding leaf was being measured, the leaves immediately below this leaf of two or three other plants in the same pot were excised and cut into pieces. Representative samples of eight pieces (about 50 mg) each were placed in sucrose solutions (about 0.5 ml) graded in Ψ in steps of 1 bar. The direction of the change in density of the solution was determined after the tissue had been in contact with the solution for 30 to 40 min (12). The tissue Ψ was interpolated to one-fourth bar. Determinations were run in duplicate, which usually agreed within 1 bar and also with measurements made with a pressure chamber (2) on the same leaf.

Measurement of Soil Water Potential. Soil Ψ was monitored while leaf elongation was being measured. Since soil Ψ was changing considerably with time, thin nylon Bouyoucus resistance units (3) with a minimal lag time were used. These units are also much more sensitive than gypsum blocks to changes in soil moisture around field capacity. Each unit was calibrated by coating with a slurry of 5% (w/v) $CaSO_4 \cdot 2H_2O$ and equilibrating in a dialysis sac sequentially against a series of solutions of Carbowax 6000 (Union Carbide Co.) of increasing concentrations. After equilibrium was reached, as indicated by constant resistance, the Ψ of the external solution was determined with a vapor pressure osmometer. The calibration curves were confirmed by data based on equilibrating the units in a pressure plate apparatus (17).

The resistance units were installed in pots 4 days before leaf elongation was measured. A small hole was dug 2.5 cm from the edge of the pot. The soil removed was mixed with 5% $CaSO_4 \cdot 2H_2O$ and used to surround and cover the resistance unit. A tensiometer (mercury manometer type) was installed in the same pot to verify the measurements within the tensiometer range. The pot was watered and carried through one drying cycle before measurements began.

RESULTS

Elongation in Well Watered Plants. We reported (13) that the growth rate of a leaf of a well watered maize plant remained remarkably constant in the growth chamber. Present work indicates that the rate also did not vary appreciably from plant to plant. Among the youngest expanding leaves of 16 plants (10 days old and well watered) varying in total length from 20 to 30 cm, the rate ranged from 53 to 61 μ/min with the majority at 59 μ/min. The coefficient of variability was only 6.3%. Nevertheless, plants were selected for expanding leaves of similar length when data were based on measurements from different plants.

Effects of Changes in Soil Water Potential. Elongation of maize leaves was highly sensitive to slight reductions in soil Ψ under the conditions used (Fig. 1). The fastest elongation was at the highest soil Ψ, −0.1 bar. The elongation rate was reduced by 19% when soil Ψ dropped to −0.2 bar and by 50% when it dropped to −0.8 bar. Elongation stopped completely as soil Ψ decreased to about −2.5 bars. It is not implied that the relationship between soil Ψ and elongation is unique. Obviously it would depend on other factors, such as the transpiration rate (13), root distribution, and soil desorption characteristics.

The response of leaf elongation to soil water depletion was dynamic, with the rate decreasing continuously as the soil Ψ decreased from the maximum. The drop in rate was perceptible over periods of tens of minutes in soil of field capacity or drier. This continuous change necessitated the simultaneous measurements of soil Ψ, leaf Ψ, and rate of elongation.

We mentioned previously (13) that elongation was sensitive to slight reductions in leaf Ψ. The complete curve relating elongation to leaf Ψ, obtained at the same time as the data in Figure 1, is given in Figure 2. Elongation decreased almost linearly with decreases in leaf Ψ and ceased when leaf Ψ reached −7 to −8 bars. The data in Figure 2 generally agree with Boyer's results on maize (5) but differ in some specifics. The initial decrease in elongation with reductions in leaf Ψ was much more gradual but complete stoppage occurred at a leaf Ψ several bars higher (more positive) than in his data. We measured the growth rate under light virtually at the instant when leaf Ψ was reduced to a particular level by transpiration and soil water depletion. Boyer measured the mean growth rate over a 24-hr period with the plant kept in a humid and dark chamber to prevent transpiration and maintain a constant leaf Ψ.

It was shown that elongation resumed within less than a minute when a mildly stressed plant was watered (13) but the estimation of response time had been complicated by the time required for water to penetrate the soil to roots and by the swelling of the soil upon wetting which displaced the base of the leaf upward. With small holes in the soil to ensure that water reached some roots in 1 sec or so and with the base of the plant secured to prevent displacement, resumption in elongation was apparent within a few seconds or less after watering (Fig. 3). The rapidity of this response is in agreement with the idea of water in the xylem acting as a hydraulic unit (13, 16) to bring about immediate changes in leaf water status when Ψ of the root medium was changed.

Raschke (16) showed that changes in hydraulic tension at the basal portion of detached maize leaves were transmitted to the upper portion within a fraction of a second, as indicated by changes in stomatal aperture. The present results indicate that the transmission of these changes is not much slower even in plants with intact roots.

The response of a fully expanded leaf under stress to watering was examined to determine the magnitude of reversible changes in leaf dimensions (in contrast to the irreversible increases in length during growth) when turgor changes. Upon watering, the stressed fully grown leaf sometimes did not change length but more often shrank first (*e.g.*, a total of 20 μ in 3 min) and then elongated slightly (*e.g.*, a total of 150 μ in 30 min). Since this reversible change is initially opposite the response of the young leaf to watering, the initial response of the young leaf must be attributed to irreversible growth, which, being larger by one or more orders of magnitude, would mask the reversible change in leaf length.

Effects of Excision. When a maize plant was excised at the mesocotyl to interrupt the water supply, the leaf initially showed a slight increase in the elongation rate (Fig. 4). This can be explained through a release of xylem tension. Elongation abruptly stopped about 10 min later and the leaf began to shrink so that 30 min after excision the leaf length had been decreased by about 200 μ.

Effects of Changing Root Osmoticum. Roots of a plant grown in nutrient solution were subjected to a sequence of alternating stress and stress release treatments with solutions of different concentrations of Carbowax 6000. Data on leaf elongation are presented (Fig. 5, a and b) for one plant. Other plants and experiments gave identical results. Prior to any treatment and with roots in 0.1 mM $CaCl_2$, the leaf elongated at 38 μ/min. Elongation slower than that of the plant in soil (Fig. 1) might be due to the higher light intensity used during the measurement. Elongation was not affected by changing the Ψ of the root medium from 0 bar to −0.5 bar but was temporarily reduced when Ψ was changed to −1.0 bar. Changing the medium to −2.0 bars reduced elongation drastically. However, the initial growth stoppage was followed by resumption at a much slower rate, suggesting possible adjustment in extensibility (10) or cell solutes. This resumption in growth was also evident when stresses of −2.5 and −3.0 bars were applied.

When stress was released by changing the root medium back to 0 bar, the leaf started to elongate immediately, with the previously described transitory rapid phase (13) preceding the slower steady state phase. At all levels of stress used in this experiment (Fig. 5), the steady state rate of growth recovered fully after stress was released. By comparison of observed leaf length with extrapolated leaf length (Fig. 5, dotted line), it is seen that the transitory rapid growth after stress release compensated completely for the slower increase in length during a stress that was mild and very short (−2.0 bars). With moderate and slightly longer stresses (−2.5 and −3.0 bars), the reduction in growth was not compensated for completely.

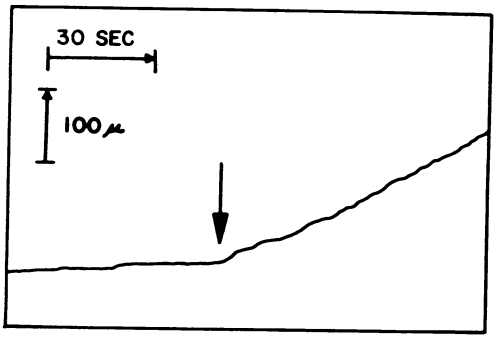

FIG. 3. Response of leaf elongation of stressed plants to watering. Measurements were made on the youngest leaf of 10-day-old plants in the growth chamber. Arrow indicates time of watering. Plant was growing in a porous planting mix perforated with four holes (6 mm diameter) to ensure rapid water penetration to the roots. The base of the plant was clamped to the frame holding the LVDT to prevent movement caused by the expansion of the planting mix and pot displacement when water was added. Prior to watering, elongation was about 16 μ/min.

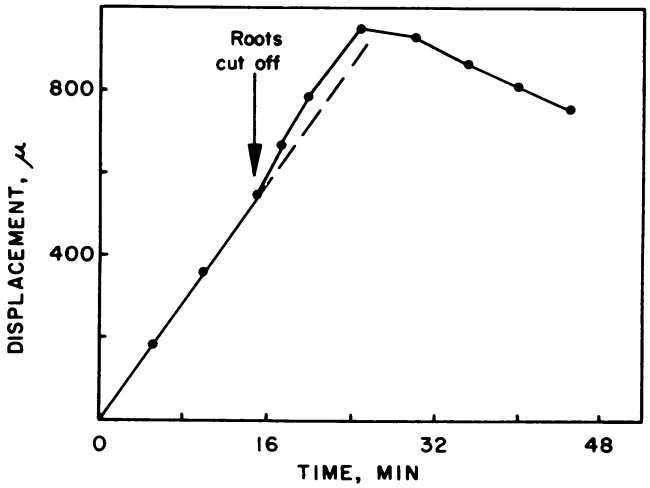

FIG. 4. Effect of excising roots on leaf elongation. Measurements were taken on the youngest (second) leaf of a 7-day-old plant in the laboratory under lights (Sylvania iodine-quartz lamps, filtered through 7 cm of water) with an intensity of 4000 ft-c. The plant was clamped at the coleoptilar node and excised at the mesocotyl.

Transitory growth responses of *Nitella* to the step-wise application and release of water stress were delineated by Green (10). For higher plants we reported on the transitory response but only for the case of stress release (13). Present data show transitory responses after stress application and demonstrate a clear but partial recovery in growth rate.

Effect on Elongation as Compared with CO_2 Assimilation and Transpiration. Recent work (5) with several plant species showed that growth totaled over a 24-hr period was more sensitive to water stress than CO_2 assimilation but data were not available for short term changes associated with stress development and release. In this study we continuously monitored leaf elongation, CO_2 assimilation, and transpiration on the same plants as their water status changed. As the soil water was gradually depleted, elongation slowed continuously and eventually stopped in a matter of hours. In contrast, CO_2 assimilation and transpiration remained almost constant during this period. Rewatering brought about a rapid resumption

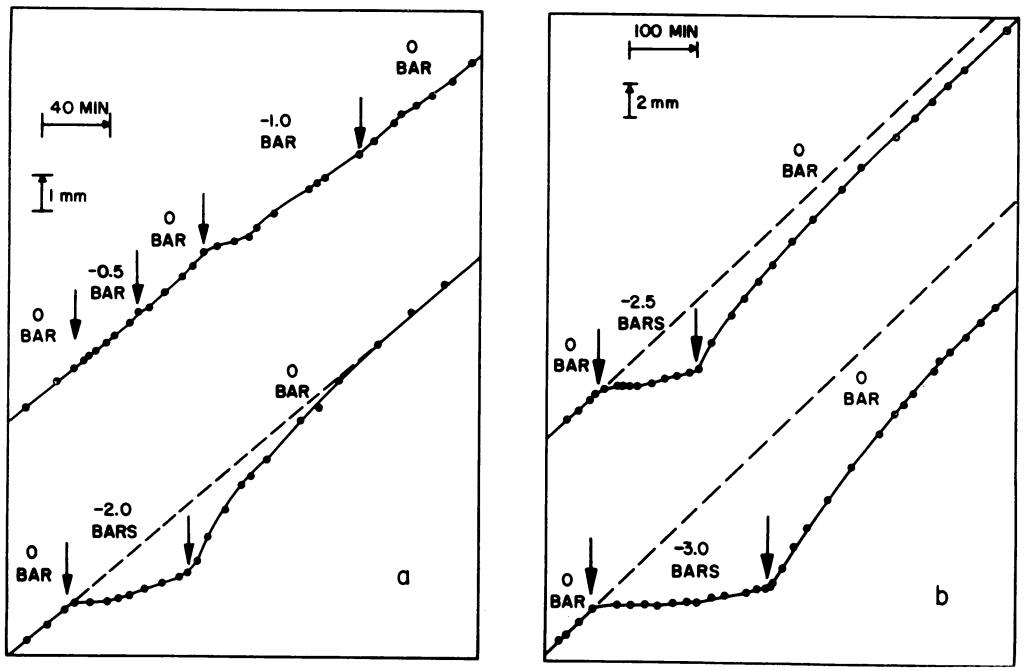

FIG. 5. Effects of step-wise changes in Ψ of the root medium on leaf elongation. Plants were 7 days old, grown in nutrient solution, and transferred to 0.1 mM $CaCl_2$ 1 day before the experiment. Carbowax 6000, purified by passing through a demineralizing column (Dr. B. E. Janes, personal communication), was the osmoticum. The Ψ of root medium (always containing 0.1 mM $CaCl_2$) was changed at times indicated by arrows. The experiment was conducted in the laboratory (4000 ft-c) with the plant clamped at the coleoptilar node. Dotted lines indicate extrapolated leaf length. Note the differences in scales between a and b.

of growth but only barely raised the steady state CO_2 assimilation and transpiration (Fig. 6, a and b). This indicates that stress severe enough to stop elongation only caused a very slight stomatal closure and probably did not affect the biochemical parameters of photosynthesis. There was a transitory decrease in CO_2 assimilation after watering (Fig. 6b) which corresponded to a transitory increase in leaf temperature (Fig. 6c) and a similar decrease in transpiration (data not shown). This behavior was probably the result of epidermal cells gaining turgor faster than guard cells after watering, thus causing a transitory closure of stomata (11).

In other experiments where stress was more severe, CO_2 assimilation was markedly reduced. After watering, both assimilation and elongation showed a lag of tens of minutes before increasing.

Effects of Longer Water Stress. The data in Figure 5 suggest that the damaging effect of stress did not persist after stress was released, for growth rate fully recovered in a short time. Only when stress was not severe and long, however, was this true. In another experiment, plants were stressed in Carbowax solutions for a relatively long period of 6 hr and then allowed to recover for 15 hr. As shown in Table I, complete recovery in growth was attained after 15 hr when prior stress had been at −0.5 or −2.0 bars, but growth remained depressed when stress had been at −3.0 and −6.0 bars. The enlargement rate of leaves of sunflower stressed for several days did not return to the control rate after watering (5).

As measured with a ruler, young leaves of plants subjected to 1 or more days of stress in soil were substantially shorter than those of control plants (Fig. 7). Although growth resumed after stress was released, final leaf lengths, including the leaf (sixth) which was not visible at the beginning of the stress period, were slightly less than in the control. Aside from this small reduction in length, the main effect of stress appeared to be the postponement of growth. The growth curve for the stressed leaf after watering was almost identical to the latter portion of the curve for the control leaf, except for its displacement to a later time (Fig. 7).

Data obtained using an LVDT showed a persistent depression in growth after plants subjected to fairly severe stress in Carbowax were placed back in water (Table I). There was probably a similar aftereffect of stress on growth in the experiment represented by Figure 7 (compare the growth of the fifth leaf on day 15 and 16). However, the aftereffect was not sufficient to be readily discernible when length was measured with a ruler. This again points to the importance of gauging elongation with methods sensitive enough to resolve short term changes.

DISCUSSION

This study provides additional evidence supporting and extending the previous conclusion (13) that leaf elongation in maize responds immediately and is extremely sensitive to changes in plant water status. A slight decrease in Ψ of the leaf resulted in slower growth. Raising the Ψ of the root medium can cause a virtually instant growth acceleration. Even excision of the root system effected a temporary increase in elongation of the leaf, presumably because of the transitory improvement in water status due to release of xylem tension. These facts all point to the crucial and direct role of water in growth; its uptake provides the physical driving force for cell enlargement.

Changes in soil Ψ within a narrow range (from −0.1 to −2.5 bars) were sufficient to stop elongation completely. The associated change in leaf Ψ was also small, about 4 bars. The observation that relatively small changes in water status cause drastic changes in growth agrees with findings of Boyer (4) on enlargement of sunflower leaves and corroborates results obtained on long term growth of maize under field (18) and laboratory (5) conditions. Also, Kleinendorst and Brouwer (14) recently found that growth of maize leaves is closely re-

lated to leaf water content as the latter was varied by changing root temperature.

Besides being sensitive to stress in the rooting medium, growth is readily affected also when leaf water balance is changed by altering evaporative demand. We have shown (13) that a sudden increase and decrease in radiation load on the plant caused growth responses, including the transitory rapid phase upon stress release, startlingly similar to effects elicited by changes in root osmoticum.

Our study clearly demonstrates for higher plants a transitory rapid growth upon stress release and a partial growth recovery upon the onset of stress. This behavior is strikingly similar to that of *Nitella* internodal cells subjected to osmotic stress and release (10). Recovery in Ψ of maize leaf after rewatering should be approximately hyperbolic with time, as shown by Boyer (4) for other plants. Therefore, the Ψ and turgor pressure of the leaf should be lower during the recovery period than in the subsequent steady state phase. Hence, an elongation rate higher in the transitory phase than in the steady state phase indicates that the extensibility of the tissue is increased by stress. In addition, the data suggest the possibility that the yield threshold (minimal yield stress, see Ref. 10) of the cell of a higher plant may be lowered substantially by water deficit.

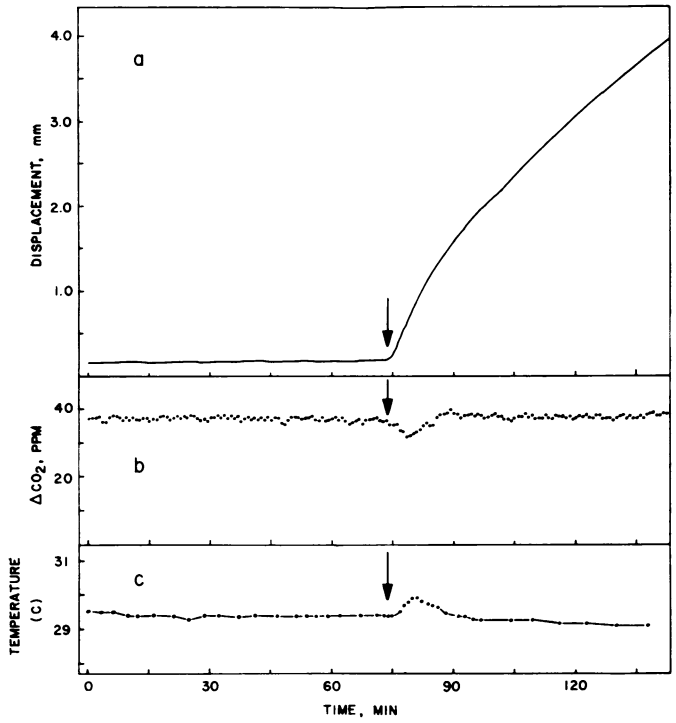

FIG. 6. Effects of mild water stress and stress release on elongation (a), CO_2 assimilation as indicated by differences in CO_2 content of air before and after passing over the leaves (b), and temperature of leaves (c) of 11-day-old plants growing in soil. Arrows indicate the time of watering. The youngest (fourth) leaf was monitored for elongation. The next older (third) leaf of the same plant, together with the third leaf of another plant in the same pot, were placed in a leaf chamber and monitored (1) for CO_2 assimilation, transpiration, and leaf temperature. The experiment was carried out in the laboratory under lights (2100 ft-c at the chamber) described in Figure 4. The flow rate through the chamber was 3.4 l min^{-1}. Mean rates of steady state CO_2 assimilation were 24.7 and 25.7 mg dm^{-2} hr^{-1}, respectively, shortly before and after watering. Mean rates of steady state transpiration were 1.16 and 1.23 g dm^{-2} hr^{-1}, respectively, before and after watering. Data were corrected for lag times of apparatus.

Table I. *Recovery of Leaf Elongation in 15 hr after 6 hr of Stress*

Ψ of Stress Medium[1]	Elongation Rate after:	
	6-hr stress	6-hr stress + 15-hr recovery[2]
bars	*% of rate before stress*	
−0.5	42	101
−2.0	37	100
−3.0	6	86
−6.0	0	55

[1] Roots of the plants were placed in solutions of Carbowax 6000.

[2] Roots were placed back for 15 hr, including a 9-hr dark period, in one-tenth strength Hoagland solution for recovery.

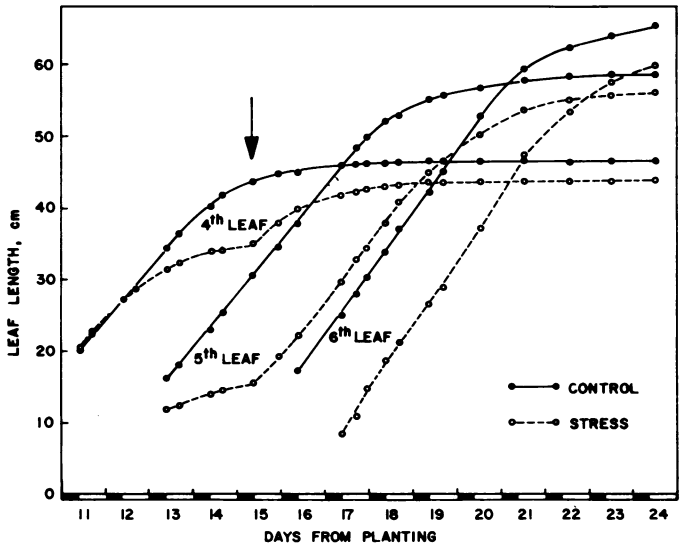

FIG. 7. Effects of long term water stress on leaf elongation. Two plants were grown in the growth chamber in each pot containing 1.8 liter of a planting mix of high water holding capacity in order to allow a relatively long yet not too severe stress. Stress was initiated by withholding water on the morning of the 12th day. Arrow indicates time of watering of stressed plants. Solid bars indicate dark periods. Lengths were measured periodically with a ruler from the apex of the particular leaf to the ligule of the second leaf, which served as a reference base level since the second leaf had fully matured. Data are means of four plants (two pots).

A growth of stressed plants faster than the control after rewatering has been discussed in the literature in connection with the supposed ability of plants to compensate partially for previous stress (*e.g.*, Ref. 7 and 8). Our data (Fig. 7), however, indicate that the growth after watering is merely the resumption of a postponed event. Although in one period the growth rate is faster than in the control, it is due to slowed growth of the control leaves upon reaching maturity, not to accelerated growth of the previously stressed leaves. The truly compensatory rapid growth elucidated (Fig. 5) is very transitory, lasting only a fraction of an hour, and hence does not contribute significantly to the total length of the leaf.

The importance of favorable water status and turgor in expansive growth was recognized many years ago (15). With recent emphasis on the molecular and metabolic aspect of stress physiology, however, the role of turgor as a physical

force needed for growth has been almost overlooked at times (6, 9). In studying the causal relations between water deficits and plant processes, one must differentiate early and late events among the numerous changes in stressed plants. Since plant processes are generally highly integrated, the direct effect of stress on one process must lead, in time, to changes in numerous others. Determination of the sequence of events at the onset of stress would aid in differentiating the primary effects from secondary and tertiary effects.

Among the earliest known metabolic changes at the onset of water stress are reductions in polyribosome level and CO_2 assimilation. However, Hsiao (12) reported that changes in polyribosomes seem to follow the change in growth, not precede it. The reduction in CO_2 assimilation is at least partly the result of stomatal closure, a turgor-mediated process. Yet the present data show that as stress develops in maize, growth is completely stopped before CO_2 assimilation is affected noticeably. Growth is also stopped before there is any noticeable increase in ribonuclease or amylase in the tissue (T. C. Hsiao and W. Segel, unpublished data). Hence, the reduction in growth is not the result of changes in these metabolic parameters, at least not during the initial period of stress. Rather, the decrease in growth is most likely the direct result of a lack of turgor needed for cell expansion.

This conclusion is also strongly supported by the data shown in Figure 5a. Although growth was severely checked by the short and mild stress (−2.0 bars), the effect on leaf length was completely compensated for by the transitory rapid growth upon stress release. Metabolic processes necessary for cell expansion apparently proceeded unchecked during the short period of stress and reduced growth.

In view of the extreme sensitivity and immediate response of expansive growth to changes in water status, it is plausible that many of the observed metabolic alterations caused by water stress arise indirectly as a result of reduced growth.

Acknowledgments—We thank Miss Jean Koskela for technical assistance and Dr. Herman Wiebe for valuable suggestions.

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